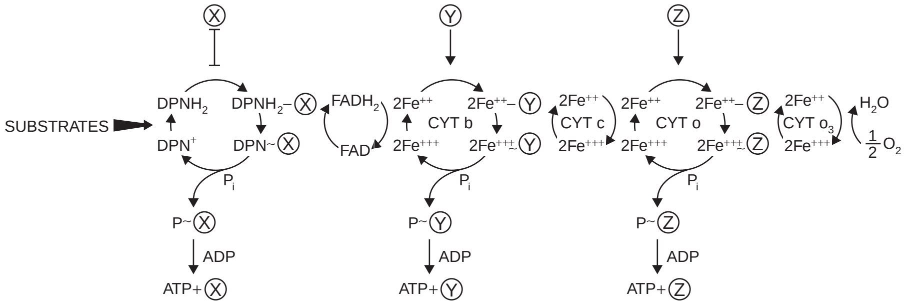


Figure 6.5. Lehninger's conception of the coupling of the electron transport chain with oxidative phosphorylation via high-energy intermediates. X, Y, and Z are three different enzymes, $P_i$ is inorganic phosphate, ∼ is a high-energy bond, and other substances are carriers undergoing reversible oxidation-reduction. Reproduced from A. L. Lehninger et al. (1958), Oxidative phosphorylation, *Science, 128*, 450–6, Figure 3, p. 455.

With this account of the final step, Lehninger and his colleagues considered two possible mechanisms (their term) for the generation of X∼P. By one account it was the reduced carrier (e.g., the cytochrome receiving the pair of electrons) that entered into a high-energy bond with the enzyme, whereas by the other it was the oxidized carrier (the cytochrome surrendering the electrons) that formed the high-energy bond. Appealing again to evidence from exchange reactions, specifically, that the reactions occurred at a maximal rate when the carriers were kept in a fully oxidized state, but not in a reduced one, Lehninger and his colleagues concluded that the second proposal was correct. Although expressing caution as to how decisive the evidence was, they interpreted their results as supporting the mechanism shown in Figure 6.5 according to which, at each of the three phosphorylation sites, an enzyme bound itself to the reduced carrier. When the carrier was then oxidized, the bond between the carrier and the enzyme became a high-energy one. At the first site, for example, the oxidation resulted in DPN∼X. Inorganic phosphate then replaced the carrier (DPN) in the bond, yielding P∼X. Finally ADP replaced the enzyme (X), yielding ATP and X. Once this type of reaction sequence had occurred at all three sites, and the energy-depleted electrons had joined with hydrogen ions and oxygen to make water, one round of oxidative phosphorylation was achieved. Energy was now stored in high-energy phosphate bonds in several molecules of ATP and was available for a variety of purposes.

At this point, both Green and Lehninger had succeeded in segregating submitochondrial particles and had proposed accounts of the operations involved in the mechanism of oxidative phosphorylation. Efraim Racker then attempted to take the endeavor a step further by isolating a soluble enzyme that was



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